

PHOTOPERIODIC AND TEMPERATURE REGULATION OF DIAPAUSE IN *LABIDOCERA AESTIVA* (COPEPODA: CALANOIDA)

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ABSTRACT

The calanoid copepod *Labidocera aestiva* was reared in the laboratory to ascertain the effects of photoperiod and temperature on subitaneous and diapause egg production. The results indicate that photoperiod is the primary stimulus regulating the type(s) of eggs produced by a female, but that the temperature regimen can modify this effect. Under short daylength photoperiods (e.g., 8L:16D) subitaneous egg production is increased by increasing the temperature regimen from 15.0°C or 19.0°C to 25.0°C. However, under long daylength regimens (e.g., 18L:6D) females appear to be unresponsive to temperature changes within the range of 15.0°C to 25.0°C. It is suggested that this response to photoperiod and temperature more accurately couples the life cycle of *L. aestiva* with seasonal environmental fluctuations.

INTRODUCTION

Research investigations of the last 10 years have made it increasingly evident that many marine calanoid copepods and other zooplankton have dormant stages (Onbe, 1978; Paranjape, 1980; Coull and Grant, 1981; review by Grice and Marcus, 1981). Diapause stages are a critical phase in the life cycle of these animals because they make possible long-term survival during periods unfavorable for continuous development. Elucidation of factors that influence the induction, maintenance, and termination of diapause should make possible more accurate predictions of seasonal fluctuations in the composition of plankton communities, and provide life history information needed to model and manage marine ecosystems.

At the northern edge of its range in Vineyard Sound, MA, *Labidocera aestiva* occurs seasonally in the plankton (Fish, 1925; Marcus, 1979). Adults appear in early summer and give rise to a series of overlapping generations. Nauplii, copepodites, and adults disappear from the plankton by the end of December, but the species remains in the area as a benthic diapause egg. The seasonal production of subitaneous and diapause eggs by *L. aestiva* in Vineyard Sound has been documented (Marcus, 1979), and it has been demonstrated for laboratory-reared females that photoperiod influences the type(s) of eggs produced (Marcus, 1980, 1982).

The results reported herein substantiate the importance of photoperiod as a factor regulating the phenology of *L. aestiva*. The data indicate that a short daylength photoperiod (e.g. 8L:16D) is the primary cue that triggers diapause egg production, but that the temperature regimen can modify this effect. The influence of these two environmental parameters on the life history pattern and population biology of *L. aestiva* in Vineyard Sound is discussed.

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MATERIALS AND METHODS

Labidocera aestiva individuals were reared from the first naupliar stage to reproductive maturity in 19 l glass carboys. The apparatus and procedure for rearing the nauplii, copepodites, and adults of *L. aestiva* is described in Marcus (1980). The same schedule for feeding, transfer of animals to clean seawater, and egg collection was followed throughout this study.

Experimental populations were initiated in each carboy with 200 nauplii derived from subitaneous or chilled diapause eggs. The eggs were produced by freshly collected females from Vineyard Sound or by females reared (first or second generation) in the laboratory. The animals in each carboy were reared at a constant temperature (14.5° , 18.0° , or $24.0^{\circ} \pm 1.0^{\circ}\text{C}$) and photoperiodic regimen (8L:16D, 12L:12D, or 18L:6D). Nine different combinations of photoperiod and temperature were analyzed. Seven were examined in this study, and two previously (Marcus, 1980). Two to five replicate experiments were conducted for each combination. When egg production began, the number of males and females in each carboy was equalized at 20–30 copepods of each sex. This was done by filtering the contents of the carboy according to the usual procedure (see Marcus, 1980) and removing adults at random from the filtrate with a wide-mouth pipette.

Eggs were collected from each carboy every 2–3 days for 6–14 days. For each collection a sample of 100–120 eggs from the total number of eggs obtained from the carboy that day, was placed in a dish containing glass fiber filtered seawater and incubated at 25.0°C and 12L:12D to hasten the time to hatching. After 4–5 days (initial) the number of hatched eggs was determined. The unhatched eggs were placed in jars containing filtered seawater and chilled at 5.0°C for a minimum of 40 days. At the end of this interval, the eggs were warmed at 25.0°C and the number that hatched (final) was ascertained. The proportion of subitaneous eggs produced was calculated by dividing the initial hatch by the total number of eggs in the sample. The proportion of diapause eggs produced was calculated by dividing the final hatch by the total number of eggs in the original sample. The remaining portion was classified as non-viable. All values were converted to percentages to facilitate comparison between samples and replicate carboys. Overall values for subitaneous, diapause, and non-viable egg production for each carboy were calculated as the mean of values for each collection day. After arc sine transformation of the percentage values, the analysis of variance was used to test for significant differences between means. Body size was estimated by preserving a minimum of 20 adult males and 20 females from each carboy in 5% buffered formalin, and subsequently measuring them to determine cephalothorax and total length.

RESULTS

The ages of laboratory-reared *Labidocera aestiva* at the onset of egg production were 26.6 ± 3.1 days at 13.5° – 15.5°C , 21.5 ± 3.4 days at 17.0° – 19.0°C , and 16.4 ± 2.4 days at 23.0° – 25.0°C . More than 60% of the individuals survived to adulthood in each experimental carboy. The total number of eggs removed from a carboy was determined for most, but not all days that eggs were collected. Values ranged from several hundred to a few thousand eggs in each carboy per day. For some carboys the number of eggs collected per day varied by an order of magnitude. However, these differences had no obvious influence on the proportions of subitaneous, diapause, and non-viable eggs produced because the values were comparable in all instances.

The percentages of eggs that hatched initially at 25.0°C and that which hatched after prolonged exposure to 5.0°C are shown for each carboy in Tables I and II.

TABLE I

Percent hatch of eggs produced by females reared at 23.0°C–25.0°C under 8L:16D, 12L:12D, or 18L:6D. Eggs that did not hatch within 4–5 days at 25.0°C (initial) were incubated in jars at 5.0°C. The final hatch of these eggs at 25.0°C is indicated, as well as the cephalothorax (CT) and total body (TL) lengths in millimeters attained by adult males and females for each carboy. \bar{X} = mean \pm S.E. The blanks indicate that no eggs were incubated.

Photo-period	Percent hatch (\pm S.D.)			Adult size attained (\pm S.D.)			
	Carboy no.	Initial 25°C	Final 5°C	Female		Male	
				CT	TL	CT	TL
8L:16D	1	21.5 \pm 25.2	87.5 \pm 1.9	1.48 \pm .06	1.98 \pm .08	1.43 \pm .04	1.89 \pm .08
	2	37.5 \pm 16.3	80.5 \pm 13.5	1.48 \pm .04	1.98 \pm .05	1.41 \pm .07	1.84 \pm .06
	3	17.6 \pm 12.0	82.3 \pm 3.8	1.55 \pm .05	2.06 \pm .07	1.51 \pm .05	1.96 \pm .07
	4	51.8 \pm 21.1	79.1 \pm 2.8	1.46 \pm .04	1.96 \pm .06	1.40 \pm .03	1.82 \pm .05
X		32.1 \pm 7.9	82.4 \pm 1.8	1.49 \pm .02	2.00 \pm .02	1.44 \pm .02	1.88 \pm .03
12L:12D	5	81.0 \pm 14.0	87.5 \pm 8.5	1.59 \pm .05	2.10 \pm .06	1.43 \pm .06	1.88 \pm .05
	6	61.5 \pm 29.0	45.0 \pm 2.7	1.65 \pm .05	2.20 \pm .04	1.57 \pm .01	2.10 \pm .01
	7	65.5 \pm 15.3	14.0 \pm 14.0	1.59 \pm .01	2.15 \pm .04	1.53 \pm .03	2.05 \pm .01
	8	62.0 \pm 20.4	18.0 \pm 0.0	1.73 \pm .07	2.32 \pm .10	1.51 \pm .07	2.07 \pm .08
X		67.5 \pm 1.6	41.1 \pm 16.9	1.64 \pm .03	2.19 \pm .05	1.51 \pm .03	2.03 \pm .05
18L:6D	9	90.0 \pm 3.2	2.0 \pm 2.0	1.47 \pm .05	1.95 \pm .06	1.42 \pm .05	1.85 \pm .06
	10	84.3 \pm 6.0	—	1.51 \pm .07	2.01 \pm .09	1.43 \pm .07	1.86 \pm .09
	11	88.7 \pm 5.5	—	1.53 \pm .10	2.03 \pm .11	1.45 \pm .05	1.94 \pm .07
	12	91.8 \pm 2.5	—	1.51 \pm .08	1.99 \pm .08	1.44 \pm .05	1.89 \pm .06
	13	91.5 \pm 2.5	—	1.56 \pm .06	2.08 \pm .08	1.48 \pm .05	1.98 \pm .07
X		89.3 \pm 1.4	2.0 \pm 2.0	1.52 \pm .01	2.01 \pm .02	1.44 \pm .01	1.90 \pm .02

For each photoperiodic and temperature regimen the F values for the transformed data are less than the tabular values at the 5% level and therefore indicate no significant differences between the means of replicate carboys. The average percentages of subitaneous, diapause, and non-viable eggs produced at each photoperiodic and temperature combination are depicted in Figure 1. The values shown for 8L:16D and 18L:6D at 13.5°–15.5°C were derived from the results of Marcus (1980). The type(s) of eggs produced was affected primarily by photoperiod. Regardless of temperature, the greatest percentage of subitaneous eggs was produced at 18L:6D. Within the framework of a 24 h regimen, as the period of light was reduced (and dark increased) the percentage of subitaneous eggs declined, while the percentage of diapause eggs increased. For example, at 23.0°–25.0°C subitaneous egg production varied from 89.3% at 18L:6D to 67.5% at 12L:12D, to 32.1% at 8L:16D. Diapause egg production for these same conditions was 0.2%, 13.4%, and 55.9% respectively. The same trend in the types of eggs produced was observed for the experiments conducted at 17.0°–19.0°C, and at 13.5°–15.5°C (see Marcus, 1980). For all but one combination of photoperiod and temperature, 10.5–19.6% of the eggs were non-viable. The exception, 13.5°–15.5°C and 12L:12D, had a high proportion of non-viable eggs (35.1%) and an unexpectedly low percentage of diapause eggs (15.9%). However, the percentage of subitaneous eggs was not unusual.

The temperature regimen to which animals were exposed affected the types of eggs produced less than did photoperiod (Figure 1; Tables I, II). For the two cooler

TABLE II

Percent hatch of eggs produced by females reared at 17.0°–19.0°C under 8L:16D, or 12L:12D and 18L:6D and at 13.5°–15.5°C under 12L:12D. Refer to Table I for an explanation of the hatch and size data.

Photo-period	Carboy no.	Percent hatch (\pm S.D.)		Adult size attained (\pm S.D.)			
		Initial 25°C	Final 5°C	Female		Male	
				CT	TL	CT	TL
Temperature 17.0°–19.0°C							
8L:16D	14	14.4 \pm 8.7	69.8 \pm 5.8	1.60 \pm .07	2.08 \pm .31	1.50 \pm .06	1.96 \pm .08
	15	14.0 \pm 5.6	83.7 \pm 7.8	1.64 \pm .09	2.17 \pm .11	1.53 \pm .07	1.97 \pm .08
X		14.2 \pm 0.2	76.7 \pm 6.9	1.62 \pm .02	2.13 \pm .05	1.52 \pm .02	1.97 \pm .01
12L:12D	16	52.3 \pm 25.1	79.0 \pm 9.1	1.49 \pm .06	1.97 \pm .09	1.43 \pm .06	1.88 \pm .08
	17	47.3 \pm 16.0	68.3 \pm 2.7	1.57 \pm .06	2.09 \pm .08	1.46 \pm .05	1.90 \pm .07
X		49.8 \pm 2.5	73.7 \pm 5.3	1.53 \pm .04	2.03 \pm .06	1.45 \pm .02	1.89 \pm .01
18L:6D	18	90.3 \pm 4.9	0.0	1.56 \pm .06	2.05 \pm .06	1.46 \pm .07	1.90 \pm .09
	19	86.0 \pm 6.1	2.0 \pm 2.0	1.53 \pm .06	2.04 \pm .08	1.47 \pm .10	1.89 \pm .08
X		88.2 \pm 2.2	1.0 \pm 1.0	1.55 \pm .02	2.05 \pm .01	1.47 \pm .01	1.90 \pm .01
Temperature 13.5°–15.5°C							
12L:12D	20	53.8 \pm 19.4	18.5 \pm 9.0	1.73 \pm .09	2.34 \pm .06	1.67 \pm .07	2.34 \pm .06
	21	56.5 \pm 16.8	7.8 \pm 10.7	1.72 \pm .08	2.37 \pm .12	1.62 \pm .05	2.22 \pm .08
	22	34.5 \pm 17.1	14.0 \pm 8.4	1.70 \pm .08	2.32 \pm .09	1.60 \pm .04	2.13 \pm .08
	23	51.3 \pm 4.1	84.2 \pm 6.3	1.64 \pm .05	2.19 \pm .07	1.57 \pm .07	2.07 \pm .11
X		49.0 \pm 5.0	31.1 \pm 17.8	1.70 \pm .02	2.31 \pm .04	1.62 \pm .02	2.19 \pm .06

regimens (13.5°–15.5°C, and 17.0°–19.0°C) the percentage of subitaneous eggs produced was comparable at each photoperiodic regimen, but at 23.0°–25.0°C the percentage of subitaneous eggs produced was markedly greater for the two shorter photoperiodic regimes (8L:16D and 12L:12D). At 18L:6D no temperature effect was observed. The percentage of diapause eggs obtained was minimal (0.2%) under 18L:6D at both 17.0°–19.0°C and 23.0°–25.0°C.

The body length of adult males and females reared in replicate carboys for each combination of photoperiod and temperature were similar (Tables I and II). For each experimental regimen females were longer than males (both cephalothorax and total length). Body length was inversely correlated with temperature. For the two cooler regimens body length and day length were inversely correlated, however, this relationship was not evident at 23.0°–25.0°C (Figure 2).

DISCUSSION

This study demonstrates the primary importance of photoperiod as a trigger for the induction of diapause in *Labidocera aestiva*, and a compensatory role for temperature. This is the first report of such an interaction for a marine copepod, although this relationship has been shown for many terrestrial and freshwater arthropods (Danilevsky, 1965; Hutchinson, 1967; Mansingh, 1971; Watson and

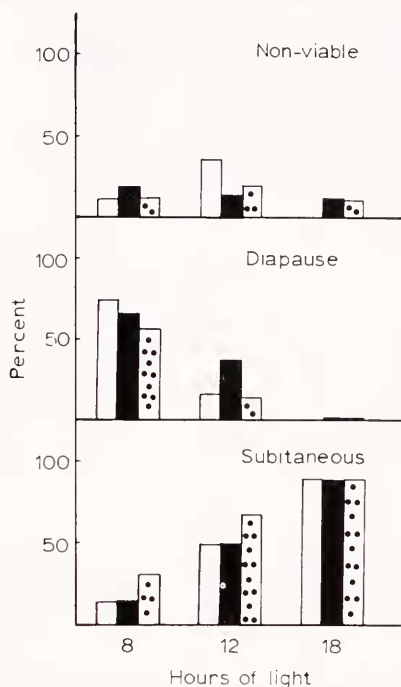


FIGURE 1. Subitaneous, diapause, and non-viable egg production (percent) by females reared under 8L:16D, 12L:12D, and 18L:6D at 13.5°–15.5°C (white), 17.0°–19.0°C (black), and 23.0°–25.0°C (dots). At 13.5°–15.5°C and 18L:6D only subitaneous egg production was determined.

Smallman, 1971; Beck, 1980). For each temperature regimen tested, the proportion of diapause eggs produced by the laboratory-reared *L. aestiva* was greatest at 8L:16D and declined as the period of experimental daylength was increased. This response was balanced by a reverse trend for subitaneous egg production. The percentages of subitaneous and diapause eggs produced was most affected by photoperiod, and the values are comparable to values reported for animals collected from Vineyard Sound at times of the year with correspondingly equivalent daylength periods (Marcus, 1979, 1980). Subitaneous egg production is maximal under long daylength conditions which prevail during the summer, whereas diapause egg production is greatest under periods of short daylength during the fall. Although photoperiod is the primary factor controlling diapause and subitaneous egg production, temperature may modify this influence. Within the range of temperature (15.0°–19.0°C) usually encountered in Vineyard Sound during September and October, the proportion of subitaneous eggs produced by laboratory-reared copepods is similar for any given photoperiod. However, for short daylength periods (e.g., less than 12L:12D), warm temperatures (e.g., 25.0°C) induce a greater proportion of subitaneous eggs (Table I; Figure 1). These photoperiods prevail in Vineyard Sound after mid-September until the vernal equinox. If water temperatures were unseasonably warm one fall, then the usual decline in subitaneous egg production should be postponed or more gradual. This would enable the population to take advantage of the longer growing season due to warmer temperature and maximize the number of individuals in that year's population. Although the effect of temperatures below 13.5°C were not investigated, if water temperatures were

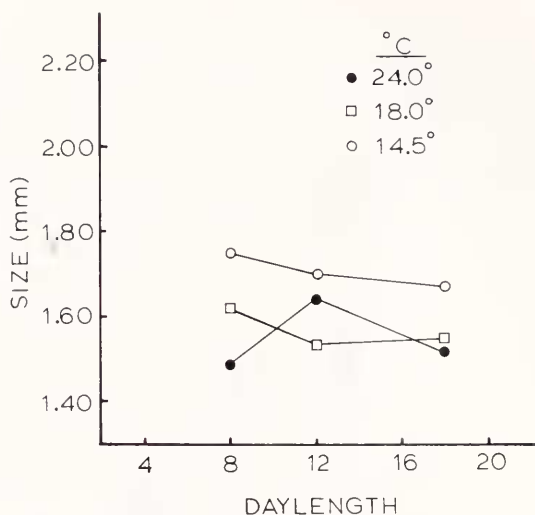


FIGURE 2. Cephalothorax length of adult females reared in the laboratory under different photoperiod and temperature regimens. The period of light is indicated. Temperatures are $\pm 1.0^{\circ}\text{C}$.

unseasonably cold the reverse effect might occur, so that diapause egg production would increase earlier in the year. This response would ensure a maximum number of individuals in the next year's population. Adult *L. aestiva* disappear from the plankton by mid-December and do not appear again in Vineyard Sound until late May or June. At this time water temperatures are usually 15.0° – 20.0°C and daylengths exceed 12 hours. Under long day photoperiods (e.g., 18L:6D) in the laboratory, the type(s) of eggs produced is unaffected by temperatures of 15.0° – 25.0°C . These results suggest that if water temperatures are unseasonably cool during the spring and early summer in Vineyard Sound, *L. aestiva* will nevertheless continue to maximize subitaneous egg production, and thereby promote rapid increase in the population size of the species during the summer. I have studied the population of *L. aestiva* in Vineyard Sound since 1977 and have never obtained diapause eggs from early summer females (Marcus, 1979; and unpublished observations). Thus under natural conditions the combined influence of photoperiod and temperature should more accurately couple the type(s) of eggs produced by *L. aestiva* with year to year environmental fluctuations.

The body lengths attained by males and females under the different temperature regimens are similar to the sizes of animals collected in Vineyard Sound (Marcus, 1979). The laboratory reared specimens also express an inverse relationship between body size and temperature as documented for *L. aestiva* from the field (Deevey, 1960; Marcus, 1979). Interestingly, for the two cooler regimens tested in the laboratory there also appears to be an inverse correlation between body length and daylength (Figure 2). This trend was noted previously by Marcus (1980). Two explanations suggested then to account for the observed relationship were that photoperiod influences body length indirectly either by affecting the thermal regime in the laboratory incubator, or the period of grazing activity and thus food consumption. These two hypotheses are applicable to the present investigation. A third possible mechanism is that photoperiod directly determines body size by affecting specific growth rate processes. Although temperature is probably the most impor-

tant factor regulating body size of copepods (Coker, 1933; Ayccock, 1942; Deevey, 1960), it has been shown for several insects (see review by Beck, 1980) and aquatic crustacea (Sandoz and Rogers, 1944; Auvray and Dussart, 1966; Starkweather, 1976; Dalley, 1980; Steele, 1981) that photoperiod directly influences some physiological, behavioral, developmental, and reproductive processes. Further experiments conducted under carefully controlled conditions specifically with regard to diet and temperature should help to clarify this intriguing and important problem.

The findings of the present and previous (Grice and Gibson, 1975; Marcus, 1979, 1980) investigations of *L. aestiva* suggest that the diapause response of marine copepods is analogous to the response of many terrestrial and freshwater arthropods (see reviews by Hutchinson, 1967; Elgmork and Nilssen, 1978; Beck, 1980). As in many of these organisms, the embryonic diapause of *L. aestiva* is triggered by a temperature compensated photoperiodic response. Other factors such as food quality or quantity, and the numerical density of *L. aestiva* may modify this induction response, but this has yet to be demonstrated for this species nor for any other marine crustacean. There are also similarities in regard to the maintenance and termination of diapause. The duration of the refractory phase (Watson and Smallman, 1971) is reduced by exposing diapause eggs to cold temperatures. Such treatment results in synchronous hatching once the eggs are subjected to warmer temperatures (Marcus, 1979). Like insects the life cycle stage that is dormant varies among copepods. Embryonic diapause is expressed by several calanoid copepods (see review by Grice and Marcus, 1981), and naupliar (Coull and Dudley, 1976), copepodite (Marshall and Orr, 1955; Davis, 1976) and adult (Coull and Grant, 1981) dormant stages are known for harpacticoid, cyclopoid, and other calanoid copepods.

From an evolutionary standpoint it is intriguing that a wide variety of organisms in the terrestrial, freshwater, and marine systems have evolved parallel adaptations and life history cycles to cope with environmental (biotic and abiotic) adversity. In some instances the pattern of variation of the selective factor is comparable (e.g. seasonal fluctuations of temperature), and the regulation of the response is similar (e.g. shortday photoperiodic response). However, not all environmental factors vary in the same way in each system. In terrestrial systems, small ponds, and the marine intertidal, water is a limiting factor, and during the dry periods many organisms undergo diapause. These stages are highly resistant to desiccation. However, diapausing organisms inhabiting large lakes and the marine subtidal do not experience comparable periods of dryness. It would be valuable to determine whether the diapause stages of these animals are also resistant to desiccation, or whether they reflect some other attribute which is uniquely associated with their aquatic habit. Another parameter that differs among these habitats is the daily temperature regimen. In the terrestrial system many animals are exposed to a thermoperiod coincident with the day-night cycle. For some of these animals (see Beck, 1980) the temperature of the dark phase, but not the light phase, influences the diapause response. Such, daily temperature fluctuations are generally minimized in the ocean, and thus marine zooplankton may not reflect a parallel response. On the other hand, in thermally stratified waters zooplankton that migrate vertically might experience diurnal differences in temperature. If such animals moved into surface waters at night to feed and descended to deep waters during the day they would experience warmer temperatures at night than during the day. This daily thermoperiod would be the opposite of that encountered by animals in the terrestrial system and nighttime temperatures might influence the diapause response of such organisms in the reverse direction. Differences such as these might lead to subtle

but distinct variations in the expression of diapause by organisms that dwell in the terrestrial, fresh water, and marine systems.

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